

TEN-YEAR SUPPLEMENT TO "ANT LARVAE: REVIEW AND SYNTHESIS"

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Abstract.—A previous review and synthesis of published information on ant larvae is brought up to date. The same general format as the earlier review is used to relate them more readily to users.

Since our Memoir No. 7 "Ant Larvae: Review and Synthesis" was published in 1976, we have studied the larvae of 20 genera and 85 species. So much new material necessitates a partial revision, the purpose of this supplement. We have followed the same plan as in Memoir 7 and also given page references, so that any part of one may be quickly related to the corresponding part of the other. Three new topics have been added: Importance of Larvae, Changes in Nomenclature, The Future.

AVE ATQUE VALE (p. 1)

In paragraph 2 change 850 to 986 and 475 to 825.

Change paragraph 3 (in part) to read: "... it has appeared in 67 papers scattered through 15 journals over a period of 58 years ..." Add 3 journals: American Entomological Society, Transactions (5); Australian Entomological Society, Journal (1); New York Entomological Society, Journal (3). Change *Psyche* to 16 and Journal of the Kansas Entomological Society to 2.

HISTORY (p. 1)

In our chapter on "Larvae of Social Insects" (1979a) we used material and figures from Memoir 7 (1976). In a key (1979a: 315 and 1979b: 10) we separated for the first time ant larvae from those of other social insects:

- 1a. Larvae not reared separately in cells but together in nest chambers; hairs usually conspicuous on head and body 2
- 1b. Larvae reared in separate cells; hairs none or few and minute; temporal sulci present; antennae nearly always at or below lower third of cranium 3
- 1c. Larvae reared in separate cells; hairs few and minute; temporal sulci absent; antennae at lower third of cranium *Microstigmus comes*
- 2a. Body J-shaped; anterior half stout and strongly curved ventrally; posterior half straight and tapering to a sharp point; temporal sulci present; antennae usually on lower third of cranium ... Allodapoid Anthophoridae

- 2b. Body any one of diverse shapes but never as above; temporal sulci absent; antennae usually on upper half of cranium Formicidae
- 3a. Body straight; diameter greatest at AI and AII; gradually attenuated toward posterior end and more rapidly toward anterior end; each in a separate cell of a paper comb; usually hanging head down Vespidae
- 3b. Body stout, not straight; not in separate cells 4
- 4a. Thorax and AI bent ventrally; abdomen straight and of nearly uniform diameter; opening of sericteries without lips; nests in soil or rotten wood; cells lined with wax Halictidae
- 4b. Body crescentric; opening of sericteries with conspicuous lips; cells constructed of wax or of a mixture of wax and pollen Apidae

HISTORY AND METHODS (p. 1)

We now prefer 70% alcohol. If tax-free alcohol is not available, rubbing alcohol (ethyl but *not* isopropyl) may be used.

Drawing (p. 1).—Line drawings are not difficult to make: see our 1960a. Inking, however, does require more skill, which can be acquired with practice. We now use polyester drafting film, India ink for film and Rapidograph drawing pens for film (sizes 000, 0 and 1); the Hunt mapping pen is still good for details such as hairs on the body. The great advantage of film is that errors can be erased or carefully scraped off with a knife. French curves are useful but—as usual—must be carefully fitted to the desired curve.

The Scanning Electron Microscope (p. 1).—Photographs made by a scanning electron microscope (SEM) are now popular, although their use sometimes appears to be superfluous. In this regard, we cite the article by Clark and Glavog (1976: 1361). SEMs are especially useful when it is desirable to magnify higher than can be done with a light microscope, e.g. surface features of the integument. We find that any whole larva or any detail that can be seen under a light microscope can be shown more clearly with a photomicrograph or a line drawing. An example of the superiority of line drawings over SEMs is to be found in Kempf (1975).

LITERATURE (p. 1)

As the next-to-last sentence in the first paragraph insert “They total 1298.”
In the last line change 577 to 632.

MATERIAL STUDIED (p. 1)

We have studied the larvae of 777 species in 202 genera representing 51 of the 61 tribes and all 10 of the living subfamilies. The taxa are given in Appendix B. A summary by subfamilies of the number of genera and species (in parentheses) follows: Dorylinae 6 (23); Leptanillinae 2 (3); Cerapachyinae 5 (11); Myrmeciinae 2 (31); Ponerinae 41 (169); Pseudomyrmecinae 4 (34); Myrmicinae 94 (299); Aneuretinae 1 (1); Dolichoderinae 14 (54); Formicinae 33 (154).

GEOGRAPHICAL DISTRIBUTION (p. 2)

Additions only.—AFRICA—Angola 2, Cameroon 2, Ghana 3, Ivory Coast 5, Kenya 3, Madagascar 5, Morocco 1, South Africa 2, Tunisia 1, Zambia 1.
ASIA—India 4, Japan 3, Malaya 1, Singapore 1.

AUSTRALIA—New South Wales 2, South Australia 1. (It is significant that our supply of larvae has been greatly reduced as a result of Australia's restrictions on export of scientific material and the red tape attendant thereon.)

CENTRAL AMERICA—Costa Rica 9, Panama 1.

EUROPE—Spain 2.

MALAY ARCHIPELAGO—Borneo 6, Celebes 9, New Guinea 2, Philippines 1, Indonesia 1.

OCEANIA—New Hebrides 1.

SOUTH AMERICA—Brazil 15, Chile 3, Colombia 2, Ecuador 3.

UNITED STATES—Alabama 2, Florida 3, Texas 2.

WEST INDIES—Guadelupe 1.

MORPHOLOGY (pp. 2–45)

Color (pp. 4–5)

Under "green" add: *Leptothorax obturator* "a peculiar greenish tint."

Body Shape (p. 8)

On page 8 after the third line insert: ADVICE.—We recommend that in descriptions of ant larvae the profile type and mandible shape be followed by our definition of that type or shape, e.g., "Larvae pheidoloid (i.e., abdomen short, stout and straight; head ventral near anterior end, mounted on a short stout neck, which is the prothorax; ends rounded, one more so than the other." It is insufficient and inaccurate to say "like *Pheidole*": that is merely the derivation of the term.

Page 8. 1. POGONOMYRMECOID—Add *Mystrium*, *Plectroctena* to PONERINAE and delete *Stigmatomma*. Add to MYRMICINAE: *Eutetramorium*, *Goniomma*, *Hylomyrma*, *Lordomyrma*, *Octostruma*, *Terataner*; delete *Colobostruma*, *Dilobocondyla*. Add to FORMICINAE: *Acantholepis*, *Acropyga*, *Colobopsis*, *Cataglyphis*, *Proformica*, *Teratomyrmex* and change *Plagiolepis* to *Anoplolepis*.

2. PHEIDOLOID—Under MYRMICINAE add *Antichthonidris*, *Ochetomyrmex*; delete *Oligomyrmex* and *Paedalgus*. Under FORMICINAE add *Aphomyrmex*, *Petalomyrmex*. Delete DOLICHODERINAE: *Engramma*.

3. DOLICHODEROID—Add to definition "diameter approximately half the distance from labium to anus." Add *Engramma* and *Turneria* to DOLICHODERINAE; change *Dorymyrmex* to *Conomyrma*.

4. ATTOID—Change definition to read: "Short, very stout, plump, slightly curved, with both ends broadly rounded; anterior end formed by the enlarged dorsum of prothorax; head ventral, near anterior end; no neck; somites indistinct; diameter approximately equal to distance from labium to anus." Occurrence.—MYRMICINAE: *Nothidris*, *Proatta* and tribe Attini.

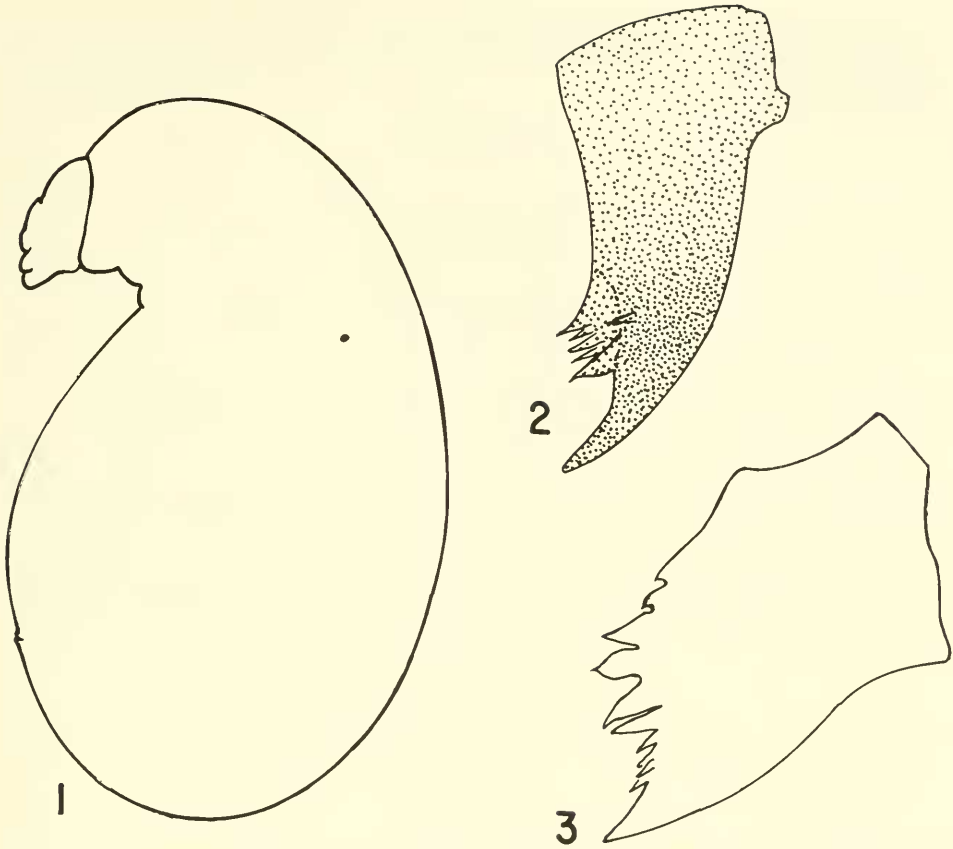
5. MYRMECIOID—MYRMECIINAE: Add *Nothomyrmecia*. PONERINAE: Add *Apomyrma*. MYRMICINAE: Add *Adlerzia*.

6. CREMATOGASTROID—Change *Cryptocerus* to *Zacryptocerus* under MYRMICINAE.

7. APHAENOGASTROID—MYRMICINAE: Add *Basiceros*, *Colobostruma*, *Oxyopomyrmex*; delete *Novomessor*.

8. PLATYTHYREOID—Delete *Eubothroponera*.

11. OECOPHYLLOID—Add *Acantholepis*.



Figs. 1–3. Paedalgoid profile type to be added to Fig. 3. Figs. 2 and 3. Mandible shapes to be added to Fig. 20. 2, *Ochetomyrmecoid*. 3, *Simoponoid*.

12. RHOPALOMASTIGOID—Add *Melissotarsus*.

A NEW PROFILE TYPE 13. PAEDALGOID—Abdomen subspherical; thorax forming a stout very short neck, which is directed ventrally; anus ventral, quite far forward and with a posterior lip. Occurrence.—MYRMICINAE: *Oligomyrmex*, *Paedalgus*. Add Fig. 1 to Fig. 3 in Memoir 7.

Body Hairs (p. 22)

Insert the following as the first paragraph under “Classification of hair-types”: “If both larval and adult stages are taken into account, then ants and bees are the only major groups of aculeate Hymenoptera in which complex hairs are abundant” (Lanham, 1979:91).

Under I. A. 3. UNCINATE. MYRMICINAE: add *Basiceros*, *Octostruma*.

Under I. A. 4. ANCHOR-TIPPED change 28 to 31 in last line.

Under I. A. Add “5. FLEXUOUS SHAFT AND FAN-SHAPED TIP (about 0.37 mm long). Occurrence: MYRMICINAE—*Hylomyrma*. (See 1977: 587.)”

Under II. A. 1. c. Add at end *Ochetomyrmex*.

Labrum (pp. 36–37)

CHIOSCLERES—Add to last sentence: “in the Formicinae and *Mystrium* and *Simopelta* in Ponerinae.”

Mandibles (p. 38)

On page 39 under SHAPE:

1. ECTATOMMOID—Delete Myrmeciinae: *Myrmecia*. Add to PONERINAE: *Myopopone*, *Plectroctena*. Add to MYRMICINAE: *Antichthonidris*, *Basiceros*, *Eutetramorium*, *Goniomma*, *Lordomyrma*, *Nothidris*, *Terataner*; change *Cryptocerus* to *Zacryptocerus*. Add to FORMICINAE: *Proformica*.

2. CAMPONOTOID—2nd line, change first clause to read “forming a round-pointed slightly curved tooth.” Add to FORMICINAE: *Acantholepis*, *Acropyga*, *Aphomomyrmex*, *Cataglyphis*, *Colobopsis*, *Petalomyrmex*, *Teratomyrmex*.

3. DOLICHODEROID—2nd line, first half, change to read “distal part, which is slender, sharp-pointed and straight.” Delete *Dorylus* under DORYLINAE. Add to MYRMICINAE: *Melissotarsus*; delete *Apterostigma*, *Myrmecocrypta*. Add to DOLICHODERINAE: *Turneria*; change *Dorymyrmex* to *Conomyrma*.

4. POGONOMYRMECOID—Delete from PONERINAE: *Myopopone*. Add to MYRMECIINAE: *Myrmecia*, *Nothomyrmecia*. Add to MYRMICINAE: *Adlerzia*, *Octostruma*, *Oxyopomyrmex*; delete *Novomessor*, *Basiceros*.

5. AMBLYOPONOID—Change last clause to “with or without minute teeth on medial surface.” Add to DORYLINAE: *Dorylus*. CERAPACHYINAE: change *Eusphinctus* to *Sphinctomyrmex*. Add to PONERINAE: *Myopopone*. Add to MYRMICINAE: *Apterostigma*, *Myrmicocrypta*, *Proatta*.

6. PRISTOMYRMECOID—MYRMICINAE: delete *Macromischoides*.

7. PHEIDOLOID—MYRMICINAE: add *Macromischa*, *Paedalgus*; delete *Melissotarsus*. Add *Aphomomyrmex* in FORMICINAE.

8. PLATYTHYREOID—Delete *Eubothroponera*.

11. DINOPONEROID—Delete “without a blade.” Add to PONERINAE: *Onychomyrmex*.

12. TETRAPONEROID—Add at end *Pseudomyrmex*.

14. RHYTIDOPONEROID—Change *Plagiolepis* to *Anoplolepis*.

16. TYPHLOMYRMECOID—Add *Apomyrma*.

A NEW SHAPE TYPE “19. OCHETOMYRMECOID—With a large (about $\frac{1}{2}$ total length) sharp-pointed apical tooth; with anterior and posterior subapical teeth, between which are numerous long needle-like teeth.” Occurrence.—MYRMICINAE: *Ochetomyrmex*. Add Fig. 2 to Fig. 20 in Memoir 7.

A NEW SHAPE TYPE “20. SIMOPONOID—Subtrapeziform; without a blade; masticatory border convex and bearing one apical and several medial teeth, which are sharp-pointed and of approximately the same size, and numerous small subapical teeth.” Occurrence: CERAPACHYINAE: *Simopone*. Add Fig. 3 to Fig. 20 in Memoir 7.

NAMES CHANGED

We have not attempted to note all name changes that have been made since our first article was published in 1928—but only those that might utterly confuse the modern user who has not kept up with synonymy.

Dorylinae

Eciton (Acamatus) is now genus *Neivamyrmex*.

Eciton (Labidus) is now genus *Labidus*.

Cerapachyinae

Change *Eusphinctus* to *Sphinctomyrmex*.

Ponerinae

1. Amblyoponini

Synonymize *Stigmatomma* under *Amblyopone*.

2. Platythyreini

Synonymize *Eubothroponera* under *Platythyrea*.

4. Ectatommini

Synonymize under *Heteroponera*: *Acanthoponera* (*Anacanthoponera*) and *Paranamopone*.

Synonymize under *Gnamptogenys*: *Holcoponera*, *Emeryella*, *Stictoponera*, *Ectatomma* (*Poneracantha*), *E. (Parectatomma)*, *E. (Gnamptogenys)*.

Synonymize *Chalcoponera* under *Rhytidoponera*.

7. Ponerini

Synonymize *Euponera* (*Trachymesopus*) under *Cryptopone*.

Myrmicinae

1. Myrmicini

Pogonomyrmex: raise *Ephebomyrmex* to a genus; delete (*Forelomyrmex*) *mayri*.

2. Pheidolini

Synonymize *Ischnomyrmex* under *Pheidole*.

Synonymize *Novomessor* under *Aphaenogaster*.

13. Leptothoracini

Change *Apsychomyrmex* to *Adelomyrmex*.

Change *Leptothorax canadensis* to *L. muscorum*.

18. Cryptocerini

Change to *Cephalotini*.

Dolichoderinae

Change *Dorymyrmex pyramicus* to *Conomyrma insana*.

Transfer *pruinosis* from *Iridomyrmex* to *Forelius*.

Formicinae

4. Formicini

Formica: delete (*Raptiformica*).

9. Plagiolepidini

Raise *Anoplolepis* to a genus.

10. Camponotini

Camponotus: raise (*Colobopsis*) to a genus.

SYSTEMATICS

Family Formicidae (pp. 45-66)

Replace our characterization of Formicidae (1st paragraph p. 46) with the following:

Soft, legless, translucent white (or whitish), with 13 somites. Thorax usually attenuated to form an obvious neck, but in many genera the head is applied to ventral surface without a neck. Leg, wing and gonopod vestiges present. Ten pairs of spiracles, one pair on each T2, T3, and AI-AVIII; peritremes of various widths and sclerotizations; atrial wall smooth or with minute spinules, which are isolated or in short rows; atrial walls of various thicknesses; atrial and tracheal openings of various ratios. Integument thin and delicate, with spinules usually present on some portion. Hairs usually abundant and moderately long; often branched or hooked. Head small but distinct (though not always conspicuous); not sclerotized and of same color as body. Eyes absent. Antennae one-segmented, usually reduced to mere discoids; usually with 3 sensilla each; high on cranium, mostly at or above middle half. Labrum a fleshy flap. Mandibles and pleurostomas the most sclerotized parts of the larva. Mandibles exceedingly varied in shape and sclerotization. Maxillae each with two one-segmented projections: palp and galea, the latter with two apical sensilla; lacinia indistinct. Labium lobose and usually with a transverse spinulose welt dorsally; bearing ventrally a pair of one-segmented palps; usually a sensillum between the palp and the opening of the sericteries; the latter a ventral transverse slit. Hypopharynx usually spinulose.

LARVAE OF THE SUBFAMILIES (pp. 46-66)

Revise DORYLINAЕ.—Profile myrmecoid. Leg vestiges conspicuous as slightly raised bosses. Antennae large, each with 2 sensilla. Clypeus and labrum not clearly distinguishable from each other. Mouth parts small and with few or no spinules. Mandibles amblyoponoid or dolichoderoid (*Cheliomyrmex*).

CERAPACHYINAЕ—Change last sentence to read: Mandibles amblyoponoid or simoponoid (*Simopone*).

MYRMECIINAЕ—In the last sentence change ectatommoid to pogonomyrmecoid.

PONERINAЕ—1. AMBLYOPONINI: In the first line delete *Amblyopone*, *Stigmatomma*; insert *Mystrium*; in the last line change *Stigmatomma* to *Amblyopone*; change *Onychomyrmex* to dinoponeroid. 7. PONERINI: Add at the end "pogonomyrmecoid (*Centromyrmex*)."

PSEUDOMYRMECINAЕ—In the last sentence insert *Pseudomyrmex* in the first parenthesis; add at the end "or platythyreoid (*Pseudomyrmex*) or dinoponeroid (*Pseudomyrmex*)."

MYRMICINAЕ—2. Revise: PHEIDOLINI—Profile aphaenogastroid (*Aphaenogaster*, *Oxyopomyrmex*, *Stenamma*, *Veromessor*) or myrmecoid (*Adlerzia*) or pogonomyrmecoid (*Goniomma*) or pheidoloid (*Machomyrma*, *Pheidole*). Maxil-

lary palp shorter than galea. Mandibles pogonomymecoid (*Aphaenogaster*, *Machomyrma*, *Oxyopomyrmex*, *Stenamma*, *Veromessor*) or pheidoloid (*Pheidole*) or ectatommoid (*Goniomma*). 3. MELISSOTARSINI—Substitute for phrase in brackets “(*Rhopalomastix*) or dolichoderoid (*Melissotarsus*).” Delete “proximal tooth very stout.” Add to profiles “or attoid (*Nothidris*).” 10. PHEIDOLOGE-TINI—Change to read “Profile pheidoloid or leptanilloid (*Trigonogaster*) or pae-dalgoid (*Oligomyrmex*, *Paedalgus*).” 11. MYRMECININI—Add to profile “ex-cept leptanilloid (*Dilobocondyla*).” Add at end “*Lordomyrma*, *Myrmecina*, *Terataner*.” 15. TETRAMORIINI—Add to second sentence “except *Eutetra-morium*).” 16. OCHETOMYRMECINI—Substitute for the bracketed phrase “(*Wasmannia*) or ochetomyrmecoid (*Ochetomyrmex*).” 18. Change CRYPTO-CERINI to CEPHALOTINI and delete last clause. 19. BASICEROTINI—Add *Octostruma* to pogonomymecoid profile. Change last sentence to read: Mandibles pogonomymecoid (*Aspididris*, *Octostruma*) or ectammoid (*Basiceros*, *Eurhopal-othrix*, *Rhopalothrix*). 20. DACETINI—Revise: Profile pogonomymecoid (*Clarkistruma*, *Daceton*, *Orectognathus*) or aphaenogastroid (*Acanthognathus*, *Al-istruma*, *Basiceros*, *Colobostruma*, *Epopostruma*, *Mesostruma*) or pheidoloid (*Smithistruma*, *Strumigenys*). Mandibles pogonomymecoid (*Alistruma*, *Epopo-struma*, *Smithistruma*), ectatommoid (*Acanthognathus*, *Basiceros*, *Clarkistruma*, *Colobostruma*, *Mesostruma*, *Orectognathus*, *Strumigenys*), or dinoponeroid (*Daceton*). 24. PROATTINI—[Delete not studied]. Profile attoid but only slightly curved. Body and head hairs sparse, generally distributed. Mandibles ambly-oponoid. 25. ATTINI—Change in parenthesis to read “except amblyoponoid (*Apterostigma*, *Myrmicocrypta*).”

DOLICHODERINAE—Delete from the first line “pheidoloid (Engramma).” FORMICINAE—Line 3. Add *Acantholepis* to oecophylloid profile and insert “ectatommoid (*Proformica*).” Line 6. Change *Plagiolepis* to *Anoplolepis*. 4. FOR-MICINI—Add at end “except ectatommoid in *Proformica*.” 6. GIGANTIOPI-NI—Line 4: delete “smooth.” 9. PLAGIOLEPIDINI—Revise: Profile pogono-mymecoid (*Anoplolepis*) or oecophylloid (*Acantholepis*). Praesaepium, uncinate hairs and chiloscleres lacking. Mandibles rhytidoponeroid (*Anoplolepis*) or cam-ponotoid (*Acantholepis*). 10. BRACHYMYRMECINI—Add *Aphomomyrmex* and *Petalomyrmex* to pheidoloid profile; add another profile: dolichoderoid (*Paratre-china*). 12. CAMPONOTINI—Add to fourth sentence “(except sparsely in *Co-lobopsis*).”

KEY TO THE MATURE ANT LARVAE IN OUR COLLECTION

Add to last line on p. 71 *Oxyepoecus* and delete *Simopelta*. Delete from first line on p. 72 *Basiceros* and *Hylomyrma*.

Fit added genera into key (pp. 72–77):

Profile 1. Pogonomymecoid

- 11a. Labrum very broad (breadth 3 times length); genae bulging
..... *Dilobocondyla* in Myrmecinini
- 11b. Labrum very broad (breadth 3 times length); genae not bulging
..... *Terataner* in Myrmecinini
- 11c. Like neither of the above
Myrmica in Myrmicini, *Leptothorax* (*Mychothorax* and *Nesomyrmex*) in
Leptothoracini

- 13a. Head without hairs; body hairs long (0.05–0.2 mm), abundant and uniformly distributed *Amblyopone* in PONERINAE
- 13b. Head without hairs; body hairs short (0.03–0.1 mm), moderately numerous, except sparse on venter of abdomen *Mystrum* in PONERINAE
- 13c. Head without hairs; body hairs minute (0.013–0.06 mm) *Eutetramorium* in Tetramoriini
- 13d. Head with hairs 14
- 14f. Four hairs on dorsum of each T2, T3, AI-AV long and flexuous, with fan-shaped tip *Hylomyrma* in Myrmicini
- 14g. Body hairs of 2 types: (1) bifid to multifid, with short, straight-branched tip and (2) deeply bifid, with curled branches *Lordomyrma* in Myrmecini
- 14h. Two long uncinat hairs on dorsum of each AI-AVI, other body hairs short and denticulate *Octostruma* in Basicerotini
- 15a. Add: *Proformica* in FORMICINAE
- 15c. Each antenna minute and mounted on a teardrop-shaped base *Goniomma* in Pheidolini
- 17b. Neck long and slender, abdomen subovoidal but with ventral profile straight (all in PONERINAE from 17b through 25b) 19
- 19a. With 2–4 glabrous discoids on dorsum; typical tubercles consisting of a frustum surmounted by a spire, which is tipped with a spine-like hair *Anochetus* and *Odontomachus*
- 19b. With 2–4 glabrous discoids on dorsum; without such tubercles *Pachycondyla*
- 19c. With 2 unpaired doorknobs on dorsum *Myopias*
- 19d. With neither discoids nor doorknobs on dorsum 20
- 23c. Add *Plectroctena*
- 27a. Chiloscleres present (Tribe Camponotini) 28
- 27b. Chiloscleres lacking Tribes Formicini, Gesomyrmecini, Gigantiopini, Melophorini and Plagiolepidini
- 28a. Body hairs sparse, with a few very long whip-like hairs but without uncinat hairs *Colobopsis*
- 28b. Body hairs numerous, without long whip-like hairs but usually with a few uncinat hairs *Camponotus*, *Calomyrmex*, *Dendromyrmex*, *Echinopla*, *Opisthopsis*, *Polyrhachis*

Profile 2. Pheidoloid

- 1a. [Delete and substitute] Mandibles ochetomyrmecoid *Ochetomyrmex* in Ochetomyrmecini
- 2c. Body hairs mostly 2–3-branched; maxillae and labium with conspicuous conoidal projections *Petalomyrmex* in FORMICINAE
- 2d. Body hairs unbranched, smooth, the tip either long and flexuous or frayed *Aphomomyrmex* in FORMICINAE
- 9a. (Add *Vollenhovia* in Solenopsidini)

Profile 3. Dolichoderoid

- 1a. Mandibles amblyoponoid; body hairs numerous, branched, generally distributed *Paratrechina* in FORMICINAE
- 1b. Mandibles camponotoid; body hairs sparse, absent on sides; of 2 types:
(1) short, fine and slightly curved; (2) long, stout, sinuate, uncinata, on
dorsum *Azteca* in DOLICHODERINAE
- 1c. Mandibles dolichoderoid *DOLICHODERINAE 2
- 2a. Body without bosses *Dolichoderus*
- 2b. Body with bosses 3
- 3a. Bosses on dorsum only *Forelius*, *Froggattella* and *Iridomyrmex*
- 3b. Bosses ventral on thorax *Bothriomyrmex*
- 3c. With a pair of low bosses on prothorax and a single terminal boss ...
..... *Engramma*
- 3d. With 2 dorsal bosses; tip of abdomen narrowed abruptly as a ventral tail
..... *Turneria*
- 3e. Boss at or near posterior end of body 4
- 4a. Boss a conoidal projection just dorsal to anus *Conomyrma*
- 4b. Boss a posterodorsal knob or low swelling *Tapinoma*

Profile 4. Attoid

- 1c. Mandibles ectatommoid *Nothidris* in Solenopsidini
- 1d. Mandibles amblyoponoid *Proatta* in Proattini

Profile 5. Myrmecioid

- 1a. Mandibles simoponoid *Simopone* in CERAPACHYINAE
- 1b. Mandibles pogonomyrmecoid 6
- 1c. Mandibles diacammoid *Megaponera* in PONERINAE
- 1d. Mandibles dolichoderoid *Cheliomyrmex* in DORYLINAE
- 1e. Mandibles amblyoponoid 2
- 1f. Mandibles ectatommoid *Myopopone* in PONERINAE
- 2a. Maxillary palp bootee-shaped *Prionopelta* in PONERINAE
- 2b. Maxillary palp not bootee-shaped 3
- 3a. Maxillary and labial palps represented by 7–15 scattered sensilla
..... *Dorylus* in DORYLINAE
- 3b. Maxillary palp a conspicuous compact group of sensilla which is more
or less elevated *Eciton* in DORYLINAE
- 3c. Maxillary palp different from the above 4
- 4a. With a row of long uncinata hairs around each somite
..... *Lioponera* in CERAPACHYINAE
- 4b. Not as above 5
- 5a. Head hairs moderately numerous (50–100)
..... *Aenictus*, *Labidus* and *Neivamyrmex* in DORLYINAE
- 5b. Head hairs few (10–25)
..... *Cerapachys*, *Phyracaces* and *Sphinctomyrmex* in CERAPACHYINAE
- 6a. Body hairs sparse; antennae minute; mandibles with a single medial tooth
..... *Adlerzia* in Pheidolini

- 6b. Body hairs numerous; antennae moderately large; mandible with 2 medial teeth MYRMECIINAE

Profile 7. Aphaenogastroid

- 1c. Mandibles ectatommoid
 *Ocymyrmex* in *Ocymyrmecini*, *Basiceros* in *Basicerotini* and
 *Acanthognathus* in *Dacetini*
 2e. Some body hairs uncinata *Rhopalothrix* in *Basicerotini*
 2f. Body hairs few, short, with frayed tip (some bent)
 *Oxyopomyrmex* in *Pheidolini*

Profile 11. Oecophylloid

Delete *Oecophylla* after characterization.

- 1a. Posterior half of abdomen conspicuously tapered; body hairs whip-like or denticulate, long (0.025–0.075 mm) ... *Acantholepis* in FORMICINAE
 1b. Posterior half of abdomen not tapered; body hairs simple and very short (0.006–0.036 mm) *Oecophylla* in FORMICINAE

Profile 12. Rhopalomastigoid

Delete *Rhopalomastix* after characterization.

- 1a. Mandibles pogonomyrmecoid *Rhopalomastix* in *Melissotarsini*
 1b. Mandibles dolichoderoid *Melissotarsus* in *Melissotarsini*

DIFFERENCES IN SEX AND CASTE (p. 78)

D. Wheeler and Nijhout (1981) found that *Pheidole bicarinata* soldier larvae have prominent mesothoracic wing discs; these are suppressed in minor worker larvae.

INTERNAL ANATOMY (p. 80)

Add to end of paragraph 2: We have at last prepared our own diagram of the internal anatomy of a hymenopterous larva. See 1979:320.

LIFE CYCLE (p. 80–82)

Substitute the following for the first two sentences in the last paragraph on p. 80: One source of confusion lies in the inclusion or exclusion of the prepupa (= semipupa). This is actually the pharate stage of the pupa. Nevertheless the integument in which the pupa develops is that of the last larval instar, although the body-shape may change: the thorax usually thickens and the body becomes straighter. There must be an ecdysis in which the fully formed pupa casts off that last larval integument.

Substitute for the fourth complete paragraph on p. 81: Onoyama (1982) has prepared a table of known numbers of instars reported in the literature together with characters used and references. We repeat here his table in a modified form and bring it up to date.

COCOONS (p. 82)

Add the 2 following paragraphs under WEAVING on p. 82.

Hölldobler and Wilson (1983) have recounted in detail the behavior of workers

Table 1. Larval instars in ants.

Ant	Instars	Characters Used	Our Reference
<i>Acantholepis frauenfeldi</i>	5	larval shape and size, chaetotaxy	1982
<i>Acromyrmex octospinosus</i>	4	length, hair, diameter of spiracle	
<i>Aphaenogaster rudis</i>	5	hair distribution, shape and length	1953
<i>Brachyponera chinensis</i>	4	head width	
<i>Cataglyphis cursor</i>	3	size, diameter of T2 spiracle, hairs, head, mouth parts	
<i>Crematogaster stadelmanni</i>	3	mandible size, chaetotaxy	1976
<i>Crematogaster striatula</i>	3	chaetotaxy, diameter of spiracle	1983
<i>Formica japonica</i>	3	head length	
<i>Messor aciculatus</i>	3	chaetotaxy	
<i>Myrmica rubra</i>	3	hair density	1976
<i>Myrmica ruginodis</i>	3	hair density, maxillary palp and galea	1983
<i>Pheidole bicarinata</i>	4	hair pattern, mandible, spiracle size	
<i>Pheidole pallidula</i>	4	spiracle size, hair shape, mandible	
<i>Plagiolepis pygmaea</i>	5	body shape, chaetotaxy	1974
<i>Polyrhachis lamellidens</i>	4	head width, hair shape	
<i>Solenopsis invicta</i>	4	mouth parts	1983
<i>Tetramorium caespitum</i>	3	hair shape	
<i>Tetramorium caespitum</i>	3	head width, mandible, maxilla, chaetotaxy	

and larvae during the weaving process in the three genera mentioned above and also in the neotropical genus *Dendromyrmex*. The small colonies of *Dendromyrmex* “build oblong carton nests on the leaves of a variety of tree species in the rain forest.” The carton is “reinforced with continuous sheets of larval silk.” These authors doubt (p. 491) that the larvae of *Technomyrmex bicolor textor* Forel produce silk used in the construction of nests.

CARE (p. 85)

Insert as the last paragraph under FEEDING:
An excellent general account of feeding is to be found in Wheeler and Bailey 1920:250–275.
A new topic to be added at the end of BIONOMICS (p. 85):

MIMICRY

Cross (1965:61) stated that “The physogastric females (figs. 8, 9) of [the mite genus *Perperipes* (Pyemotidae)] differ greatly from all other pyemotids, and apparently are mimics of the doryline ant larvae among which they live.” (See also Audy et al., 1972:490.)

TAXONOMIC CONCLUSIONS (pp. 88–93)

On page 89 we listed the myrmecological uses for the study of ant larvae. We now list 2 more:

4. Distinguish instars. We regard the mature worker larva as the definitive representative of a genus or species, but we have described younger stages whenever they were available. We have rarely, however, been sure of the instars. For such determination we should have an egg ready to hatch and a larva of each instar ready to molt; in each case the next stage will be fully formed inside and, by our technique, we can see both at once. We also need the semipupa, which will show all characters of the mature larva except shape. Because such critical specimens are rarely found it behooves the collector to get as much brood as possible. But who is interested in instars? Since caste is determined in the larval stage, all biologists would like to know when and how, and someday the applied entomologist may *need* to know.

5. As an aid in taxonomy. We have always believed that ant taxonomy should be based on both larval and adult characters. Larval characters can be particularly useful when adult characters are indistinct.

LARVAL CLASSIFICATION VS. ADULT CLASSIFICATION (pp. 92–93)

Larval classification supports the following changes since the "Genera Insectorum" (1910–1925):

5. Brown (1975:4) uses our study of the larvae to support his synonymizing *Eubothroponera* into *Platythyrea*.

6. Urbani (1977:428) states that larval characters were the best justification for the separation of the Leptanillinae from the Dorylinae. ("L'elevazione a sottofamiglia dell'antica tribù *Leptanillini* è dovuta a G. C. ed E. W. Wheeler (1930), ma la migliore giustificazione di questo punto di vista la si trova nel lavoro di G. C. e J. Wheeler (1965) dove vengono accuratamente studiate le morfologie larvali delle tre specie di cui si conoscono anche gli stadi preimaginali.")

Larval classification does not support the following changes:

4. Dorylinae. The splitting of this subfamily into Old World and New World subfamilies. We have discussed this at length in our 1984 and 1985.

5. Ponerinae. Brown's 1976 reduction of the tribe Odontomichini to a subtribe. See our 1985:260.

IMPORTANCE OF LARVAE

(p. 93, add after "Taxonomic Conclusions")

We cannot give this topic the space it deserves; furthermore it is outside the main field of our research. Nevertheless it must be discussed in any comprehensive treatment of ant larvae. Fortunately Abbott (1978:236, 242–243) has given a complete and documented survey. Shorter treatments: Febvay and Kermarrec, 1981; Hunt, 1982; Peacock et al., 1950; Schneirla, 1971:141–142; Wheeler and Wheeler, 1979a:334–336; Wüst, 1973:417. For a thumbnail sketch we have found nothing better than one sentence in a 1978 review by S. C. Stearns in the *American Scientist* 66:623: "Adults ants are dependent on soluble proteins and amino acids received from the larvae, which digest protein for the whole colony."

As a finale we quote the last paragraph in our 1979 chapter on *Larvae of Social Hymenoptera*: "This brings us back again to the idea of the colony as a superorganism. The crops of all adult members of a colony have been referred to as the collective stomach of a colony. Now we have to add the larvae of ants and wasps as a sort of collective digestive gland necessary for the health of the colony."

THE FUTURE
(add after "Importance of Larvae")

Our stream of incoming larvae has dwindled to a mere trickle. Our supply from Australia has been hampered by governmental export regulations. Our American colleagues who supplied the most larvae have reduced their field activities—as have we. Our lament was well expressed by Dr. W. L. Brown years ago: "If only I could get myrmecologists to collect larvae!" So we ask our young colleagues to collect and send us larvae.

Recently we were commenting to a young colleague (who is sending us larvae) that we were not getting larvae of new genera. He retorted: "The genera you have not studied are those whose nests are found only by accident." That had not occurred to us. We know that many nests have no superstructure around the entrance, which is just a hole in the ground; some genera nest in leaf mold or duff, others in plant cavities.

So we looked up the history of 103 genera which we have not studied: 62% have been reported only once (probably the type nest or only the type specimen), 23% we consider rare, and only 15% common.

In view of the above we have the following observations to make concerning the future of the study of ant larvae. The remaining common genera will be described. Some of the "only once" and the rare will be accidentally found and described, but some will never be discovered; they may be extinct already as the result of the degradation of the habitat. The younger stages of most genera will be needed in order that instars may be identifiable. We have studied ant larvae at the generic level. There will doubtless be problems where intraspecific and interspecific differences must be studied. Investigators must also be aware of the intranidal differences. The anatomy and function of protuberances, chiloscleres and unnamed structures will be studied. Because of the importance of larvae to the well-being of the colony, the physiology and behavior of the colony with reference to the larvae must be learned. Ant larvae will play a larger role in systematics. Where adult taxonomy is dubious, larval similarities or differences will be an aid in taxonomy.

A. TAXONOMIC BIBLIOGRAPHY OF OUR PUBLICATIONS ON ANT LARVAE
(pp. 93–96) [ADDITIONS ONLY]

General

- 1976. Ant Larvae: Review and Synthesis. Entomol. Soc. Wash., Mem. No. 7. 108 pp.
- 1979a. Larvae of the social Hymenoptera. Chap. 7, pp. 287–338. *In* Social Insects. Vol. I. H. R. Hermann, ed. Academic Press, New York.
- 1979b. Larvae of some eusocial bees and wasps. Nat. Hist. Mus. Los Ang. Cty. Mus. Contrib. Sci. No. 321, 19 pp.
- 1985. A simplified conspectus of the Formicidae. Trans. Am. Entomol. Soc. 111: 255–264.

Dorylinae

- 1984. The larvae of the army ants: a revision. J. Kans. Entomol. Soc. 56: 263–275.

Cerapachyinae

- 1974a. Supplementary studies on ant larvae: *Simopone* and *Turneria*. J. N.Y. Entomol. Soc. 82: 103–105.

Myrmeciinae

- 1980a. Larval and egg stages of the primitive ant *Nothomyrmecia macrops* Clark. J. Aust. Entomol. Soc. 19: 131–137 (with R. W. Taylor).

Ponerinae

- 1976b. Supplementary studies on ant larvae: Ponerinae. Trans. Am. Entomol. Soc. 102: 41–64.
1980b. Supplementary studies on ant larvae: Ponerinae, Myrmicinae and Formicinae. Trans. Am. Entomol. Soc. 106: 527–545.
1985b. The larvae of *Dinoponera*. Psyche 92: 387–391.
1986a. Supplementary studies on ant larvae: Ponerinae. Trans. Am. Entomol. Soc. 112: 85–94.

Myrmicinae

1977. Supplementary studies on ant larvae: Myrmicinae. Trans. Am. Entomol. Soc. 103: 581–602 [Tribes: Myrmicini, Pheidolini, Cardiocondyliini, Solenopsidini, Pheidologetini, Myrmecini, Leptothoracini, Ochetomyrmecini, Basicerotini, Attini].
1980b. See above under Ponerinae. [Tribes: Melissotarsini, Solenopsidini, Myrmecini, Tetramoriini, Basicerotini.]
1983. Supplementary studies on ant larvae: Myrmecinae. Trans. Am. Entomol. Soc. 108: 601–610 [Tribes: Myrmicini, Pheidolini, Solenopsidini, Myrmecini, Meranoplini, Cephalotini, Basicerotini, Attini].
1986b. Supplementary studies on ant larvae: Myrmicinae. J. N. Y. Entomol. Soc. (in press) [Tribes: Myrmicini, Pheidolini, Crematogastrini, Pheidologetini, Leptothoracini, Tetramoriini, Cephalotini, Basicerotini, Dacetini, Attini].
1985c. The larva of *Proatta*. Psyche 92: 447–450 [Tribe: Proattini].

Dolichoderinae

- 1974a. See above under Cerapachyinae.

Formicinae

- 1974b. Supplementary studies on ant larvae: *Teratomyrmex*. Psyche 81: 38–41.
1980b. See above under Ponerinae.
1982. Supplementary studies on ant larvae: Formicinae. Psyche 89: 175–181.
1986c. Supplementary studies on ant larvae: Formicinae. J. N. Y. Entomol. Soc. 94: 331–341.

B. MATERIAL STUDIED (pp. 96–101)

(Changes in our collection since 1976; all are additions unless otherwise indicated.)

Dorylinae

Aenictus: change *martini* to *gracilis* Emery; change *turneri* to *ceylonicus* (Mayr). *Dorylus* (*Anomma*): *molesta* Gerstäcker; (*Alaopone*) sp.; (*Dorylus*) sp.; (*Rhogmus*) sp.

Neivamyrmex: *harrisi* (Haldeman), *opacithorax* (Emery), *postcarinatus* Borgmeier, *texanus* Watkins.

Cerapachyinae

Simopone: *conciliatrix* Brown.

Myrmeciinae

Nothomyrmecia: *macrops* Clark.

Ponerinae

1. Amblyoponini. *Mystrium*: *mysticum* Roger. 2. Platythyreini. Delete *Eubothroponera tasmaniensis*. *Platythyrea*: *modesta* Forel, *parallela* (F. Smith), *pilosula* (F. Smith), *tasmaniensis* (Forel), *turneri* Forel; delete *australis*, *incerta*. 3. Typhlomyrmecini. *Typhlomyrmex*: *rogenhoferi* Mayr. 4. Ectatommini. *Gnampotogenys*: *binghami* (Forel), *costata* Emery. *Heteroponera*: *dolo* (Roger). 6. Proceratiini. *Proceratium*: unidentified sp. = *avium* Brown. 7. Ponerini. *Bothroponera*: *tessierinodis* (Emery), *tridentata* F. Smith. *Brachyponera*: *luteipes* (Mayr). *Centromyrmex*: *bequaerti* Emery. *Dinoponera*: *gigantea* (Perty); change *grandis* to *mutica* Emery. *Leptogenys*: *aspersa* Ern. André, *diminuta* (F. Smith), *iridescens* (F. Smith), *kitteli* Mayr. *Mesoponera*: *ferruginea* (F. Smith). *Plectroctena*: *cryptica* Bolton, *Myopias*: *cribriceps* Emery. 8. Odontomachini. *Anochetus*: *inermis* Ern. André, *gladiator* Mayr, *princeps* Emery, *rugosus* (F. Smith), *testaceus* Forel. *Odontomachus*: *biumbonatus* Brown, *erythrocephalus* Emery, *insularis* Guérin, *simillimus* F. Smith, *tyrannicus* F. Smith, sp.; change *haematoda* to *haematodus*.

Myrmicinae

1. Myrmicini. *Hylomyrma*: *reitteri* (Mayr), sp. = *versuta* Kempf. *Manica* sp. = *yessensis* Azuma. 2. Pheidolini. *Adlerzia*: *froggatti* Forel. *Aphaenogaster*: (*Attomyrma*) sp., (*Deromyrma*) *swammerdami* Forel. *Goniomma*: *hispanicum* (Ern. André). *Oxyopomyrmex*: sp. Make *Novomessor* a subgenus of *Aphaenogaster*. Delete *Ischnomyrmex*. Add *longiceps* (F. Smith) to *Pheidole*. 3. Melissotarsini. *Melissotarsus*: *titubans* Delage. 9. Solenopsidini. *Antichthonidris*: *bidentatus* (Mayr), *denticulatus* (Mayr). *Liomyrmex*: sp. *Nothidris*: *latastei* (Emery). *Oxyepoecus*: *punctifrons* (Borgmeier), *rastratus* (Mayr); delete "one unidentified species." *Solenopsis*: *invicta* Buren, *richteri* Forel. *Vollenhovia*: sp., sp. 10. Pheidologetini. *Paedalgus*: sp. 11. Myrmecini. *Lordomyrma*: sp. *Terataner*: *alluaudi* (Emery). 12. Meranoplini. *Calyptomyrmex*: *nummuliticus* Santschi. 15. Tetramoriini. *Eutetramorium*: *mocquerysi* Emery. 16. Ochetomyrmecini. *Ochetomyrmex*: *subpolitus* Wheeler. 18. Change Cryptocerini to Cephalotini. *Cephalotes*: *alfaroi* (Emery). 19. Basicerotini. *Basiceros*: *manni* Brown and Kempf, *singularis* (F. Smith), sp. *Octostrumma*: *inca* Brown and Kempf. 24. Proattini. *Proatta* *butteli* Forel. 25. Attini. *Cyphomyrmex*: *hamulatus* Weber.

Dolichoderinae

3. Tapinomini. *Turneria: dahli* Forel.

Formicinae

4. Formicini. *Cataglyphis: bicolor* (Fabricius). *Proformica: ferrerii* Bondroit. *Teratomyrmex: greavesi* McAreavey. 9. Plagiolepidini. *Acantholepis: capensis* Mayr. *Acropyga: sp.* 10. Brachymyrmecini. *Aphomomyrmex: afer* Emery. *Brachymyrmex: admotus* Mayr, *giardi* Emery. *Paratrechina: guatemalensis* (Forel), *longicornis* (Latreille), *wojciki* Trager. *Petalomyrmex phylax* Snelling. 12. Camponotini. *Dendromyrmex: chartifex* (F. Smith).

C. ENEMIES OF ANT LARVAE (p. 102) [ADDITIONS]

Phylum Sporozoa

- Burenella dimorpha*. Parasite. *Solenopsis geminata*.

Phylum Platyhelminthes

- Anomotaenia brevis* larva. Parasite. *Leptothorax nylanderii*.

Phylum Nematoda

- Add *Pheidole* to list of hosts.

Phylum Arthropoda

Class Insecta

Order Coleoptera

- HISTERIDAE: *Euxenister caroli*. Predation. *Eciton burchelli*. *Euxenister wheeleri*. Predation. *Eciton hamatum*. *Pulvinister nevermanni*. Predation. *Eciton hamatum*.

- PSELAPHIDAE: *Adranes taylori*. Fed by ant larvae by trophallaxis. *Lasius sitkaenesis*.

Order Lepidoptera

- LYCAENIDAE: Add to prey *Myrmica*, *Oecophylla*, *Tetramorium*, *Tapinoma*. Add to predators *Liphyra brassiolis*, *Maculinea alcon*, and *M. arion*.

- PYRALIDIDAE: *Wurthia aurivillii* and *W. myrmecophila*. Predation. *Oecophylla* and *Polyrhachis*.

- COSMOPTERYGIDAE: *Batrachedra*. Predation. *Polyrhachis dives*.

Order Diptera

- CHIRONOMIDAE: *Forcipomyia*. Predation. *Formica*.

- SYRPHIDAE: *Microdon fuscipennis*. Predation. *Forelius pruinus*.

Order Neuroptera

- CHRYSOPTERIDAE: *Italo-chrysa*. Predation. *Crematogaster*.

Order Hymenoptera

- EUCHARITIDAE: *Orasema crassa*, *Orasema* sp. Parasitoid. *Solenopsis invicta*.

Class Arachnida
Order Acarina

Parasitid mites. Parasitic. New World army ants.

E. SPECIALIZATION INDICES—CHANGES AND ADDITIONS (p. 104)

SUBFAMILY DORYLINAE 26: *Aenictus* 24, *Cheliomyrmex* 27, *Dorylus* 30, *Eciton* 24, *Labidus* 22, *Neivamyrmex* 29.

SUBFAMILY CERAPACHYINAE 22: *Simopone* 24.

SUBFAMILY MYRMECIINAE 24: *Myrmecia* 24, *Nothomyrmecia* 24.

SUBFAMILY PONERINAE: TRIBE AMBLYOPONINI: *Mystrium* 14; TRIBE PONERINI: *Plectroctena* 12.

SUBFAMILY MYRMICINAE: TRIBE MYRMICINI: *Hylomyrma* 15; TRIBE PHEIDOLINI: *Adlerzia* 14, *Goniomma* 17, *Oxyopomyrmex* 15; TRIBE MELIS-SOTARSINI 32: *Melissotarsus* 33; TRIBE SOLENOPSIDINI 21: *Antichthonidris* 14, *Nothidris* 26, *Oxyepocus* 15. TRIBE PHEIDOLOGETINI: *Paedalgus* 25. TRIBE MYRMECININI 20: *Lordomyrma* 16, *Terataner* 20. TRIBE TETRA-MORIINI 12: *Eutetramorium* 11. TRIBE OCHETOMYRMECINI: *Ochetomyr-mex* 18. TRIBE BASICEROTINI 15: *Octostruma* 9. TRIBE PROATTINI 25: *Proatta* 25.

SUBFAMILY DOLICHODERINAE: *Turneria* 27.

SUBFAMILY FORMICINAE: TRIBE FORMICINI: *Cataglyphis* 15, *Profor-mica* 18, *Teratomyrmex* 14. TRIBE PLAGIOLEPIDINI 14: *Acantholepis* 17. TRIBE BRACHYMYRMECINI: *Aphomomyrmex* 13, *Petalomyrmex* 22. TRIBE CAMPONOTINI: *Colobopsis* 19.

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